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New species of *Marthamyces* and *Ramomarthamyces* gen. nov. from New Zealand and the Cook Islands

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Abstract—A leaf-spotting fungus common on *Phormium tenax* in New Zealand is described here as *Marthamyces harakeke* sp. nov. The phylogenetic analysis prepared for the description of this new species showed *Marthamyces* to be polyphyletic. To resolve this, three *Marthamyces* species from Australia and New Zealand, *M. barbatus*, *M. dracophylli*, and *M. gilvus*, are recombined in the new genus *Ramomarthamyces*. Morphologically the *Ramomarthamyces* species differ from *Marthamyces* in having paraphyses distinctly branched, rather than propoloid. A fungus common on recently fallen leaves of *Metrosideros* spp. in New Zealand has been previously referred to as *Marthamyces emarginatus*, but is recognised here as a new species, *Marthamyces metrosideri*. In addition, two new *Marthamyces* species, *M. maccormackii* on *Metrosideros collina*, and *M. renga* on *Metrosideros collina*, *Vaccinium cereum,* and *Weinmannia samoensis*, are described from the Cook Islands, and a new *Ramomarthamyces* species, *R. tuku* on *Juncus* sp., is described from New Zealand. Finally, *Naemacyclus culmigenus* is recombined in *Marthamyces*.

Key words—fungi, *Leotiomycetes*, *Marthamycetaceae*, New Zealand flax, pathogen

Introduction

A leaf-spotting fungus common on *Phormium tenax* J.R. Forst. & G. Forst. (*Asphodelaceae*) in New Zealand has been tentatively referred to as *Propolis* sp. in the literature (McKenzie & al. 1999) and on the NZFungi website (https://nzfungi2.landcareresearch.co.nz). Macroscopically the fungus recalls *Propolis* and *Marthamyces* in having ascomata immersed in host tissue, opening by several irregular slits, and the hymenial surface having

a crystalline appearance when the flaps of covering host tissue fold back. It is distinguished from most *Marthamyces* species in having bifusiform to trifusiform ascospores and in being pathogenic, but neither of these features is unique in the genus. Ascospore shape is variable in these fungi; e.g., *Marthamyces desmoschoeni* and *M. dendrobii* have swollen areas along their filiform ascospores. A pathogen of *Miscanthus* (*Poaceae*), identified as *Naemacyclus culmigenus* by Hosoya & al. (2013), is morphologically typical of *Marthamyces*, and also matches the genus *Marthamyces* phylogenetically, based on the molecular phylogenetic analysis provided in this paper.

DNA sequencing of other *Marthamyces* specimens from New Zealand, the Cook Islands, and Australia revealed several other taxonomic issues. Species placed in *Marthamyces* by Johnston (1986, 2006) separate into two distinct clades, one of which contains the type species of *Marthamyces*, *M. emarginatus*. The clade that does not contain *M. emarginatus* is segregated here into a newly described genus, *Ramomarthamyces*. Three new *Marthamyces* species are proposed, one for specimens collected from *Metrosideros excelsa* Sol. ex Gaertn., *M. fulgens* Sol. ex Gaertn., *M. kermadecensis* W.R.B. Oliv., *M. robusta* A. Cunn., and *M. umbellata* Cav. (*Myrtaceae*) in New Zealand, a second from *Metrosideros collina* (J.R. Forst. & G. Forst.) A. Gray on the Cook Islands, and a third from *M. collina*, *Vaccinium cereum* G. Forst. (*Ericaceae*) and *Weinmannia samoensis* A. Gray (*Cunoniaceae*) on the Cook Islands. A new *Ramomarthamyces* sp. is described from *Juncus* in New Zealand.

Materials & methods

The *Marthamyces* specimens studied were collected from native forests in New Zealand, the Cook Islands, and Australia. Those maintained in culture were grown from ascospores germinating on water agar plates at the time the specimens were collected. The fungarium specimens are deposited in PDD, and the living cultures in the ICMP culture collection, with both collections maintained by Manaaki Whenua – Landcare Research, Auckland (https://scd.landcareresearch.co.nz/).

DNA extraction, amplification, and sequencing followed the methods of Johnston & Park (2005). Amplification primers were ITS1F and ITS4 for ITS (White & al. 1990, Gardes & Bruns 1993), LROR and LR5 for LSU (Bunyard & al. 1994, Vilgalys & Hester 1990), NS1 and NS4 for SSU (White & al. 1990), and mrSSU1 and mrSSU3R for mtSSU (Zoller & al. 1999).

DNA sequences from the newly collected specimens were added to those available for SSU, ITS, LSU, and mtSSU from the *Leotiomycetes* taxa treated in a class-wide, 15-gene phylogeny (Johnston & al. 2019) that were not members of the order *Helotiales*. Each gene was aligned using MAFFT (Katoh & Standley 2013) as

TABLE 1. Specimens and GenBank accession numbers for the DNA sequences used for specimens of *Marthamycetaceae* in FIGS 1 and 2. Other specimens and sequences in FIGS 1 and 2 are from Johnston et al. (2019) [available through Manaaki Whenua Datastore, https://doi.org/10.7931/T5YV-BE95].

SPECIES	VOUCHER	COUNTRY	HOST	SSU	ITS	LSU	MTSSU
'Coccomyces proteae'	CBS 111703/ CBS 111704	South Africa	*Protea* sp.	—	JN712451/ JN712450	JN712515	—
	CR252M	Puerto Rico	*Disterigma humboldtii*	—	JX089385	—	—
Cyclaneusma minus	CBS 496.73	Chile	*Pinus radiata*	FJ176812	NR_153910	FJ176868	FJ190629
	ICMP 17358	New Zealand	*Pinus radiata*	KJ606669	KJ606680	KJ606674	MH698452
Marthamyces culmigenus	TNS F-41728	Japan	*Miscanthus sinensis*	—	AB745435	AB745437	AB745436
Marthamyces desmoschoeni	ICMP 17350	New Zealand	*Desmoschoenus spiralis*	KJ606670	KJ606679	KJ606673	—
Marthamyces emarginatus	ICMP 22854	Australia	*Eucalyptus* sp.	MK681769	MH921869	MK599203	MK598751
	ICMP 22622	Australia	*Eucalyptus* sp.	—	MK599209	—	—
	ICMP 22623	Australia	*Eucalyptus* sp.	—	MK599210	—	—
Marthamyces cf. *emarginatus*	ICMP 22628	Australia	*Eucalyptus* sp.	—	MK599211	—	v
	ICMP 22621	Australia	*Eucalyptus* sp.	MK681770	MK599212	MK599204	MK598752
Marthamyces harakeke	PDD 108765	New Zealand	*Phormium tenax*	MK681771	MK599213	MK599205	MK598753
Marthamyces maccormackii	ICMP 16155	Cook Islands	*Metrosideros collina*	—	MK599215	—	—
	ICMP 15831	Cook Islands	*Metrosideros collina*	—	MK599216	—	—
	ICMP 15829	Cook Islands	*Metrosideros collina*	—	MK599217	—	—

Species	Voucher	Country	Host	SSU	ITS	LSU	mtSSU
Marthamyces metrosideri	ICMP 17398	New Zealand	*Metrosideros robusta*	MH682226	MH682227	HM140558	HM143831
	ICMP 22625	New Zealand	*Metrosideros robusta*	—	MK599218	—	—
	PDD 111232	New Zealand	*Metrosideros excelsa*	—	MK599219	—	—
	ICMP 22624	New Zealand	*Metrosideros robusta*	—	MK599220	—	—
Marthamyces quadrifidus	ICMP 18329	New Zealand	*Weinmannia racemosa*	MK681772	MK599214	HM140559	HM143832
Marthamyces renga	ICMP 15830	Cook Islands	*Metrosideros collina*	—	MK599221	—	—
	ICMP 15827	Cook Islands	*Metrosideros collina*	—	MK599222	—	—
Mellitiosporium versicolor	Lantz357 (UPS)	Sweden	—	—	—	HM140560	—
Naemacyclus fimbriatus	CBS 289.61	Switzerland	*Pinus* sp.	FJ176811	—	FJ176867	—
	CBS 440.71	Spain	*Pinus* sp.	—	MH860208	—	—
Propolis farinosa	ICMP 17354	New Zealand	—	MH682223	MH682229	HM140562	HM143834
Propolis versicolor	ILLS 60497	USA	—	—	JQ256425	JN012015	—
Ramomarthamyces barbatus	ICMP 22853	Australia	*Eucalyptus* sp.	MK681773	MH921868	MK599206	MK598749
	ICMP 22620	Australia	*Eucalyptus* sp.	—	MK599223	—	—
	ICMP 22627	Australia	*Eucalyptus* sp.	—	MK599224	—	
Ramomarthamyces dracophylli	ICMP 17381	New Zealand	*Dracophyllum sinclairii*	MH698450	MH682228	MK599207	MH698450
Ramomarthamyces gilvus	ICMP 22855	Australia	*Caustis* sp.	—	MH921870	—	—
	ICMP 22626	Australia	*Lepidosperma laterale*	—	MK599225	—	—
Ramomarthamyces tuku	ICMP 22562	New Zealand	*Juncus* sp.	—	MK599226	MK599208	MK598750

implemented in Geneious 10, the ends were manually trimmed and introns were removed as necessary, and then the alignments were concatenated. Maximum likelihood analyses were run with IQ-TREE (Nguyen & al. 2015, Chernomor & al. 2016) using models selected by ModelFinder using the BIC criterion (Kalyaanamoorthy 2017) for each partitioned gene; branch support was estimated using ultrafast bootstrap analysis with 1000 replicates (Hoang & al. 2018). *Xylaria hypoxylon* and *Neurospora crassa* were used as outgroup. We also performed an ITS analysis, which included additional specimens of each species as well as DNA sequences from two GenBank accessions of *Marthamyces* specimens identified incorrectly as *Coccomyces proteae*. The ITS analysis used the same methods as the multi-gene analysis but included only the *Marthamycetaceae* specimens together with the *Chaetomellaceae* specimens treated by Johnston & al. (2019), *Chaetomellaceae* being sister to *Marthamycetaceae* in the Fig. 1 multigene analysis. The *Marthamycetaceae* taxa and genes included in the phylogenetic analyses are provided in Table 1.

Phylogeny

The higher-level taxa resolved with our four-locus analysis (SSU, ITS, LSU, and mtSSU; Fig. 1) matched those in the more data-rich analysis of Johnston & al. (2019). The monophyletic *Marthamycetaceae* included *Mellitiosporium, Propolis, Cyclaneusma, Naemacyclus,* and *Marthamyces*. Species previously named as *Marthamyces gilvus, M. barbatus,* and *M. dracophylli* formed a clade separate from the clade containing the type species of *Marthamyces,* and these species are recombined below in a new genus, *Ramomarthamyces*. A specimen identified by Hosoya & al. (2013) as *Naemacyclus culmigenus* is strongly supported as a member of the *Marthamyces* sensu stricto clade, and this species is recombined in *Marthamyces* below. Two *Marthamyces emarginatus*-like specimens collected from *Eucalyptus* leaves in Australia are phylogenetically distinct from each other, and from *M. emarginatus* as accepted here, but are not formally named as new species because each is known from only a single specimen. The *M. emarginatus*-like species from *Metrosideros* in New Zealand is recognised as a new species, described below as *M. metrosideri*.

The ITS gene tree (Fig. 2) includes additional specimens of several of the accepted species. It also includes three accessions in GenBank deposited as *Coccomyces proteae* that are misidentifications of *Marthamyces* spp. The position of *Naemacyclus fimbriatus* differs between the two trees; clarification of its relationship requires additional genes or the sampling of additional species within *Naemacyclus*.

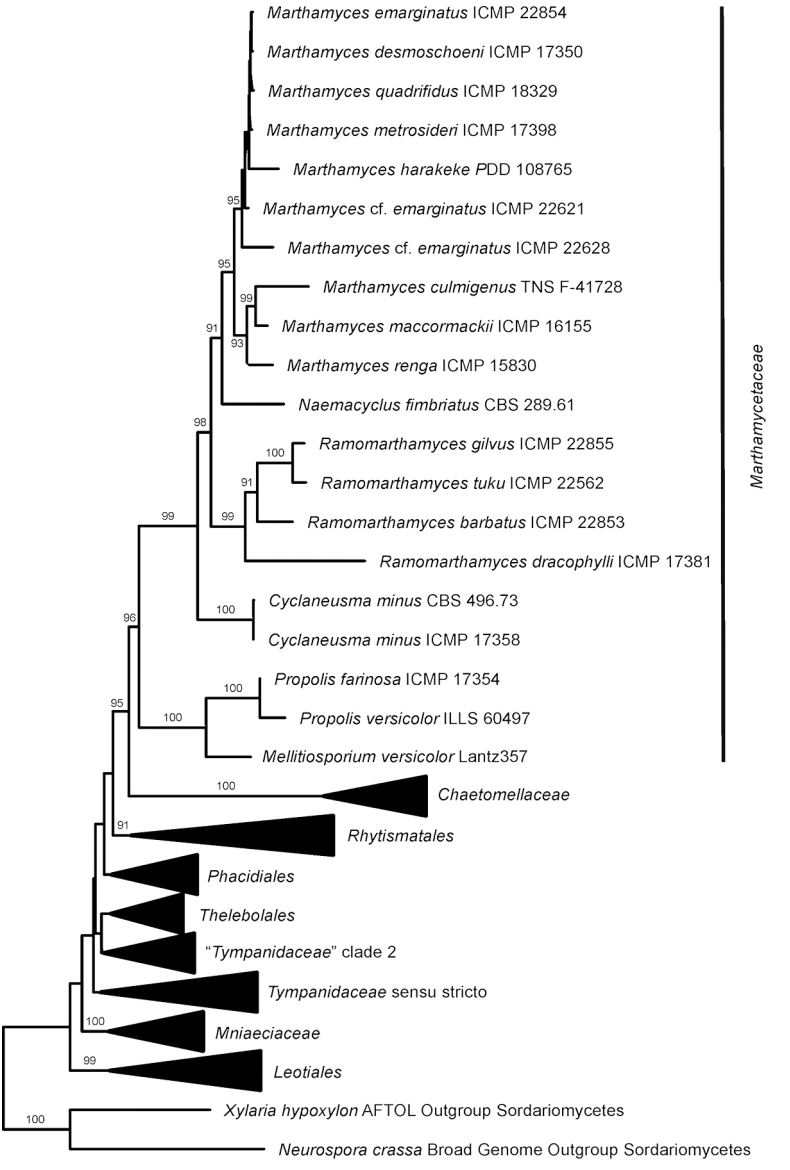


Figure 1. ML tree based on concatenated SSU, ITS, LSU, and mtSSU sequences, with bootstrap values shown when >90%. Details of the specimens of *Marthamycetaceae* included in the analysis are provided in Table 1; the extra-limital taxa in other families and orders are from Johnston et al. (2019) and their data are available though the Manaaki Whenua – Landcare Research Datastore (https://doi.org/10.7931/T5YV-BE95).

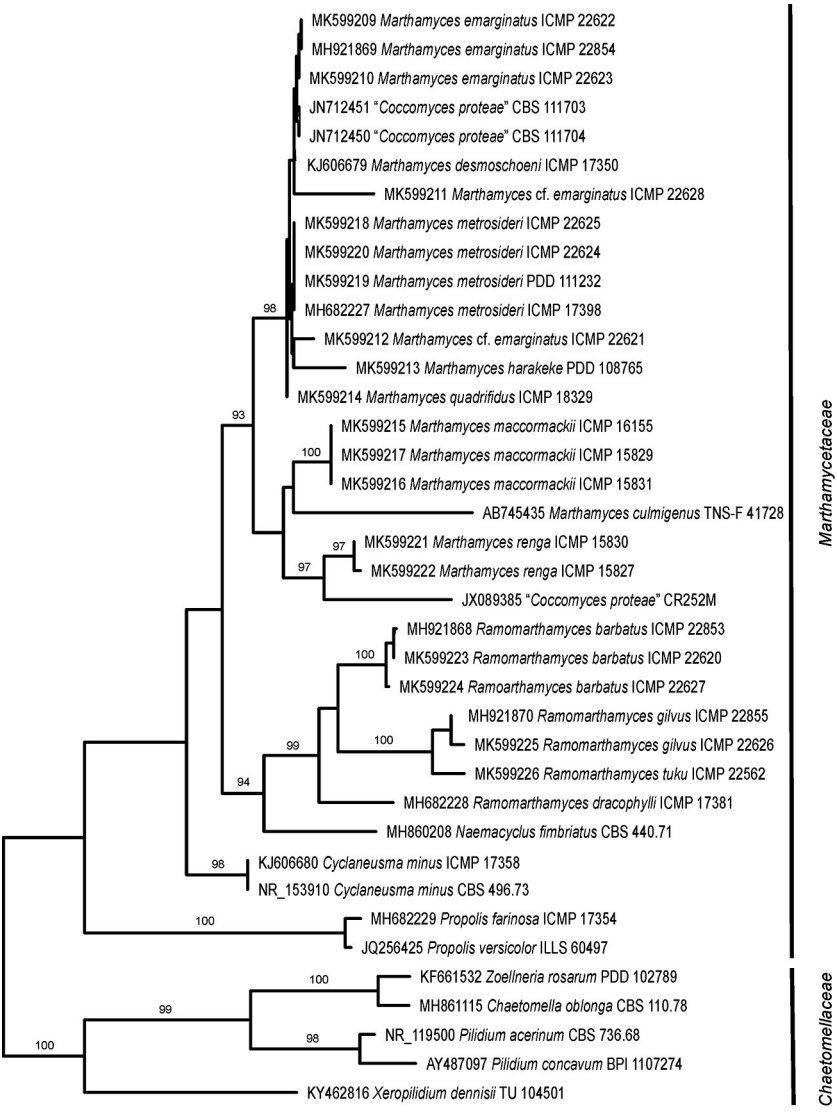


Figure 2. ML tree based on ITS sequences with bootstrap values shown when >90%. Details of the specimens of *Marthamycetaceae* included in the analysis are provided in Table 1. Members of the *Chaetomellaceae*, sister to *Marthamycetaceae* in the multi-gene analysis in Fig. 1, are used as the outgroup; data for the outgroup specimens are available through the Manaaki Whenua – Landcare Research Datastore (https://doi.org/10.7931/T5YV-BE95).

Taxonomy

Marthamyces culmigenus (Ellis & Everh.) P.R. Johnst., **comb. nov.**

IF 556322

≡ *Naemacyclus culmigenus* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 45: 151, 1893.

Notes: The combination is based on both DNA sequence and morphological data. The description of *Naemacyclus culmigenus* from Hosoya & al. (2013) cites the morphological features typical of *Marthamyces* with respect to ascomatal wall structure, the 0–1-septate filiform ascospores, and propoloid paraphyses. *Naemacyclus fimbriatus*, a heterotypic synonym of *N. pinastri*, the type species of *Naemacyclus*, differs in having unusually long periphysoids lining the upper wall of the opened ascoma, and also differs in having multi-septate ascospores and paraphyses simple at the apex (DiCosmo 1979). A specimen identified as *N. fimbriatus* (AFTOL ID-1295, CBS 289.61; Fig. 1) is phylogenetically distinct from the specimen accepted as *N. culmigenus* by Hosoya & al. (2013).

Marthamyces emarginatus (Cooke & Massee) Minter, Mycotaxon 87: 51, 2003. Fig. 3

≡ *Stictis emarginata* Cooke & Massee, Grevillea 18: 7, 1889.

≡ *Propolis emarginata* (Cooke & Massee) Sherwood, Mycotaxon 5: 323, 1977.

Specimens examined—**AUSTRALIA**: **Victoria**: on *Eucalyptus* sp., Martin 439 (K – holotype of *Stictis emarginata*). **Tasmania**: Mt Wellington, on *Eucalyptus* sp., 4 Oct 1997, coll. P.R. Johnston AU97-7 (PDD 81847, duplicate HO, culture ICMP 22621); Cradle Mountain Lake St Clair National Park, Cynthia Bay–Shadow Lake Track, near Watersmeet, on *Eucalyptus* sp., 7 Oct 1997, coll. P.R. Johnston AU97-64 (PDD 81844, duplicate HO, culture ICMP 22623); Cradle Mountain Lake St Clair National Park, Cynthia Bay–Echo Point Track, on *Eucalyptus* sp., 8 Oct 1997, coll. P.R. Johnston AU97-84 (PDD 81845, duplicate HO, culture ICMP 22622); Zeehan–Wynyard road, Hellyer Gorge State Reserve, on *Eucalyptus* sp., 12 Oct 1997, coll. P.R. Johnston AU97-123 (PDD 81846, culture ICMP 22854). **New South Wales**: New England National Park, Point Lookout, Lyrebird Walk, on *Eucalyptus* sp., 31 May 1996, coll. P.R. Johnston AU96-211-2 (PDD 81848, culture ICMP 22628).

Notes: Originally described from fallen *Eucalyptus* leaves from Australia, this species has been reported from *Eucalyptus* from the Canary Islands, North America, and South Africa (Sherwood 1977, Crous & van der Linde 1993). It was first reported from New Zealand by Johnston (1986), but on *Metrosideros* rather than *Eucalyptus*, and it has not subsequently been reported on *Eucalyptus* from New Zealand (Dick 1990, https://nzfungi2.landcareresearch.co.nz, accessed 10 October 2018). Here we accept *M. emarginatus* as a specialist of *Eucalyptus*, and the *Metrosideros*-inhabiting fungus from New Zealand is described below as a new species.

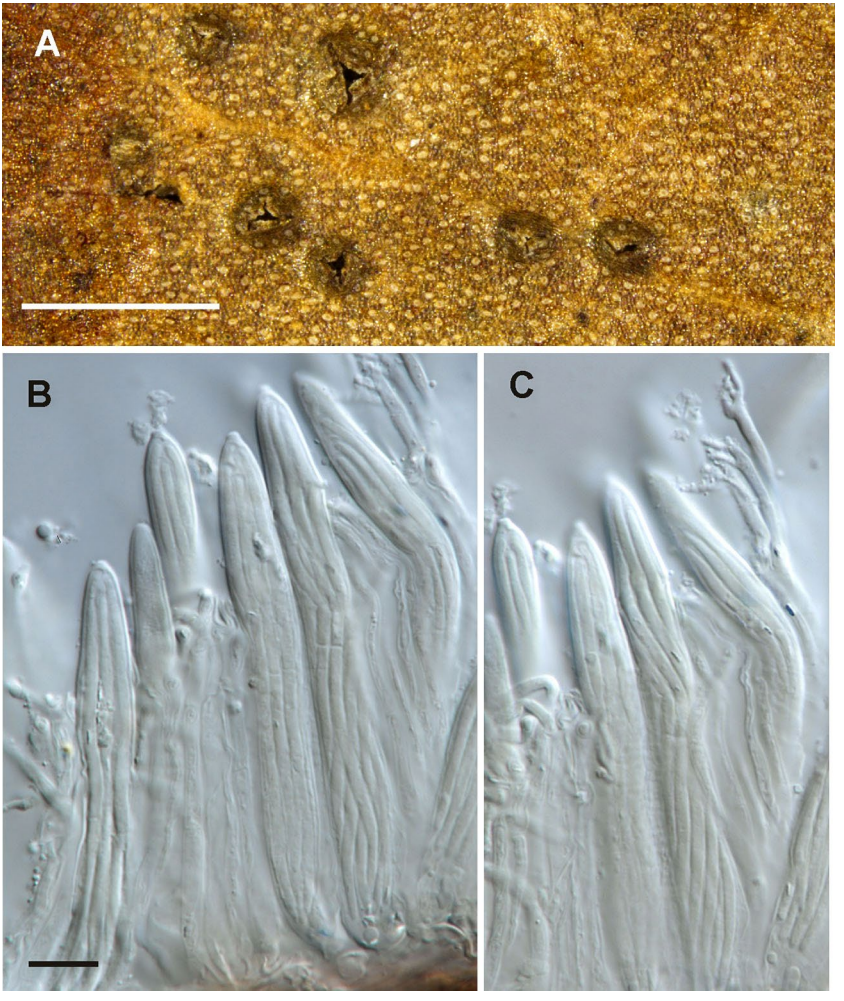


FIGURE 3. *Marthamyces emarginatus* (A. PDD 81846; B, C. PDD 81845). A. Macroscopic appearance when dry; B. Asci with rostrate apex; C. Propoloid paraphyses. Scale bars: A = 1 mm; B, C = 10 µm.

The *Marthamyces* specimens examined from fallen *Eucalyptus* leaves from Australia are similar in macro- and micro-morphology, but phylogenetically they form three groups, each probably representing a distinct species. PDD 81844 (ICMP 22623), PDD 81845 (ICMP 22622), and PDD 81846 (ICMP 22854) have almost identical ITS sequences and are morphologically more or less indistinguishable. PDD 81848 (ICMP 22628) and the three-specimen

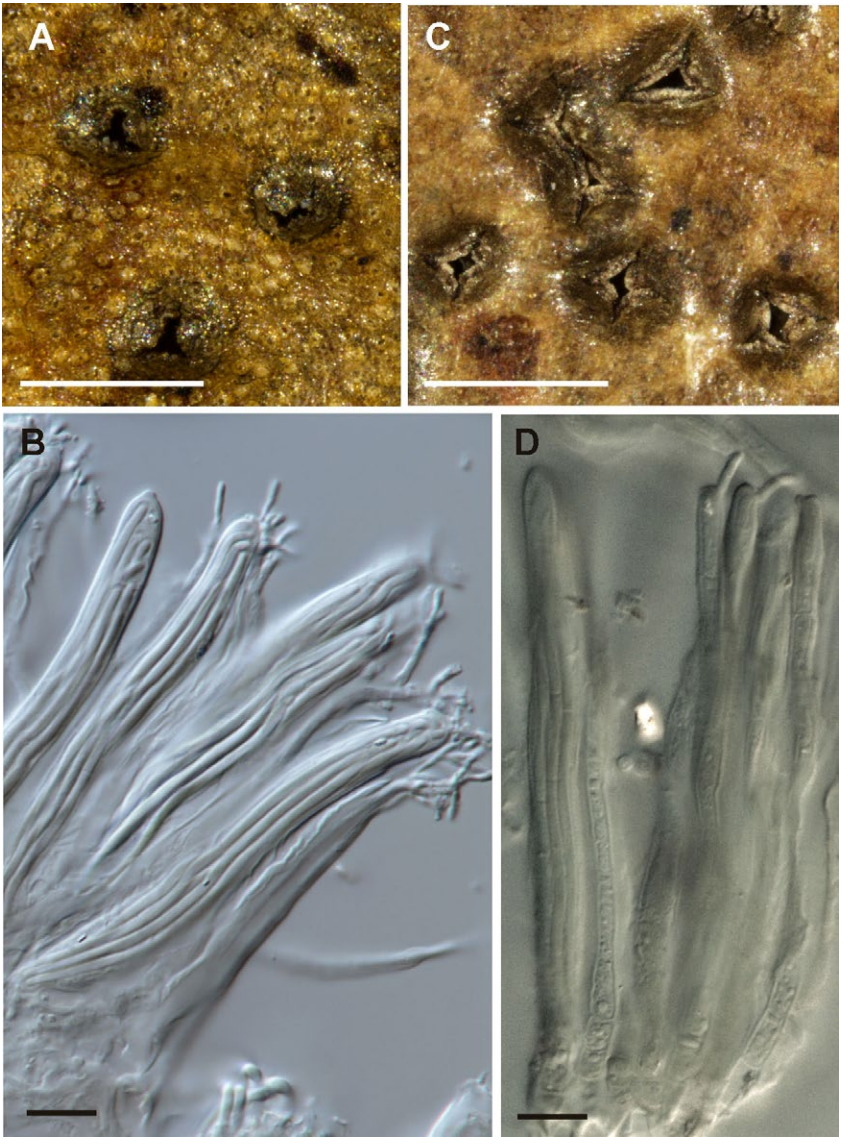


Figure 4. *Marthamyces* cf. *emarginatus* (A, B. PDD 81848; C, D. PDD 81847). A. Macroscopic appearance when dry; B. Apex of paraphyses with several long apical branches; C. Macroscopic appearance when dry; D. Paraphyses broad, sometimes with single narrow branch at apex. Scale bars: A, C = 0.5 mm; B, D = 10 µm.

group cited above share 92% identical sites across the ITS region; PDD 81848 differs morphologically in having longer, finger-like extensions at the ends of the propoloid paraphyses (Fig. 4A, B). PDD 81847 (ICMP 22621) and the three-specimen group cited above share 96% identical sites across the ITS region; PDD 81847 differs morphologically in having darker ascomata and paraphyses that are broader near the apex and typically with a single, finger-like projection (Fig. 4C, D). Here we provisionally accept the three matching specimens PDD 81844, PDD 81845, and PDD 81846 as *M. emarginatus*. No epitype is proposed because no recent specimens are available from Victoria, the type locality of *M. emarginatus*.

Marthamyces harakeke P.R. Johnst., **sp. nov.** Figs 5, 6

IF 556323

Differs from *Marthamyces emarginatus* by its *Phormium* host preference, by its fruiting on living leaves, by its ascomata being elongate, and by its broader, bifusiform to trifusiform ascospores.

Type: New Zealand: Auckland: Waitakere Ranges, Kaitarakihi Beach, on *Phormium tenax* living leaves, 20 July 1983, coll. P.R. Johnston R328 (**holotype** PDD 112252).

Etymology: harakeke, Māori name for the host.

Ascomata and conidiomata developing on living leaves within reddish, elliptic to fusiform, approximately 10–30 × 3–15 mm lesions. Ascomata more or less cylindric, 0.6–2 × 0.3–0.5 mm, concolorous with host tissue, immersed, initially with covering host tissue becoming slightly raised, then the covering host tissue splitting irregularly, the flaps of tissue folding back to expose the hymenial surface, which has a pale yellow, crystalline appearance. Undersides of flaps of host tissue also with crystals. Ascomata subepidermal, in vertical section upper wall up to 40 µm thick, comprising several layers of non-gelatinous tangled hyphae about 4–5 µm diam., with cell walls thin, pale brown, lined with a layer of periphysoids, cylindric, unbranched, 15–20 × 3–6 µm, hyaline. Periphysoids downward projecting before ascomata open, inward projecting after ascomata open, partly lost after opening. Lower wall and subhymenium 15–20 µm thick, lower wall comprising tangled hyphae 2–3 µm diam., with cell walls thin, pale brown. Paraphyses 3–4 µm diam., simple or with one or more short, tapering, narrow, 1.5–2 µm diam. branches at apex, extending about 10–20 µm beyond asci, small crystals in clumps amongst the parts of the paraphyses above the asci. Asci 110–180 × 12–14 µm, cylindric, apex broadly rounded, wall undifferentiated or slightly thinner across the apex, 8-spored. Ascospores 55–78 × 3.5–4.5 µm (1.5–2.5 µm at the constrictions), long-cylindric,

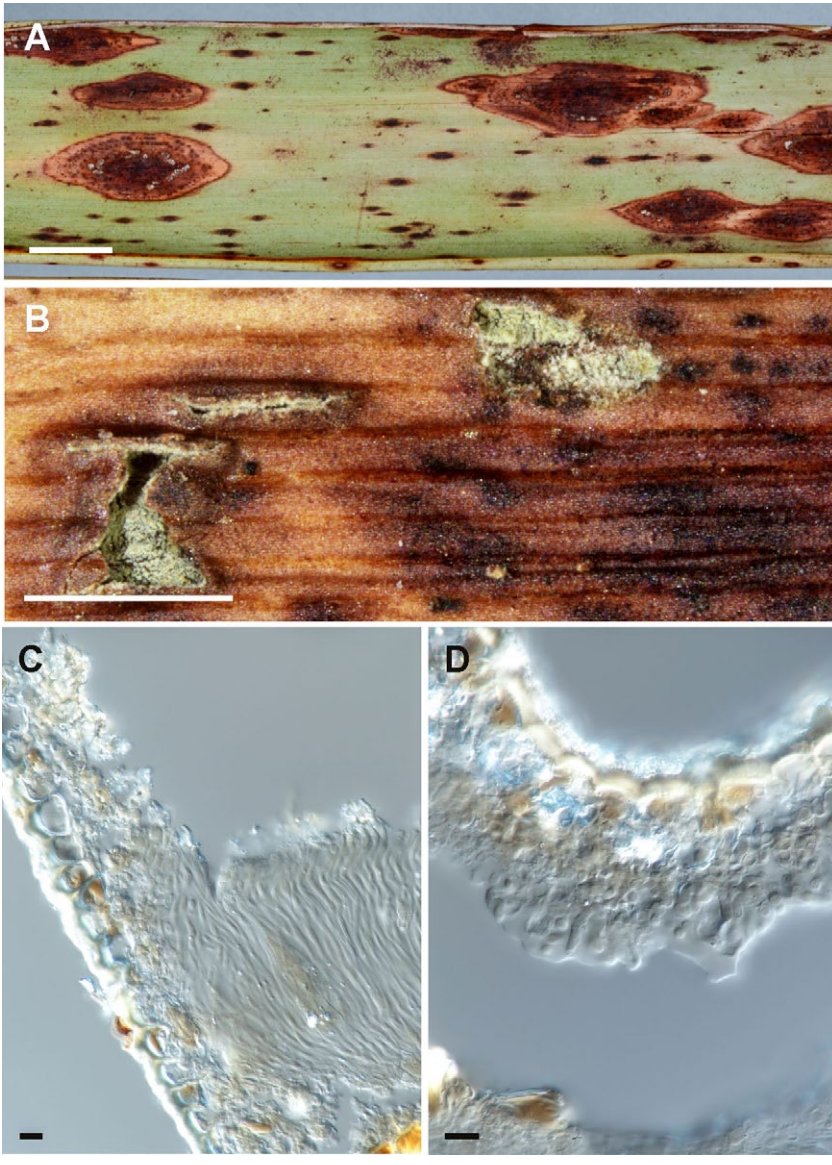


Figure 5. *Marthamyces harakeke* (A, B. PDD 108765; C, D. PDD 112252). A, B. Macroscopic appearance when dry; C. Upper wall of ascoma and part of hymenium in vertical section; D. Detail of upper wall of immature, unopened ascoma showing periphysoid layer. Scale bars: A = 1 cm; B = 1 mm; C, D = 10 μm.

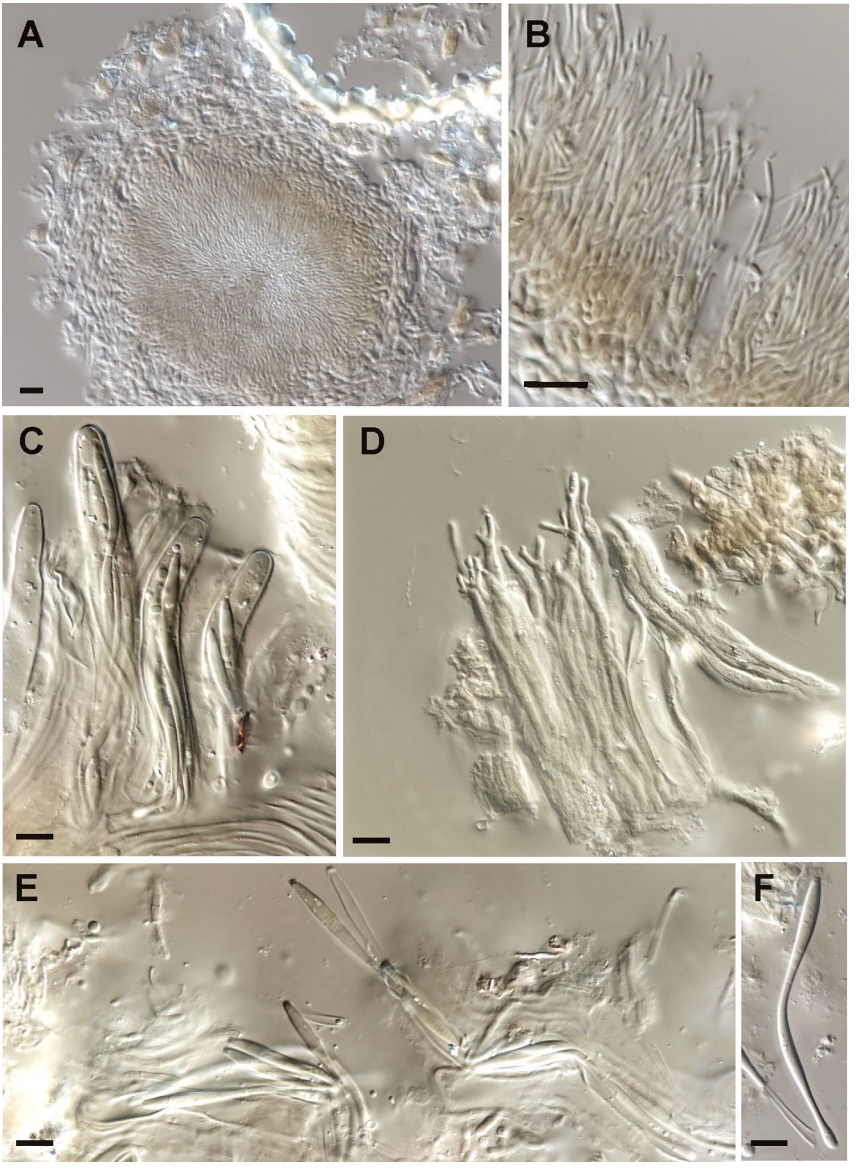


Figure 6. *Marthamyces harakeke* (A, B. PDD 112252; C–F. PDD 108765). A. Conidioma in vertical section; B. Wall of conidioma, conidiogenous cells, and conidia; C. Asci and ascospores; D. Apex of paraphyses; E, F. Ascospores with small globose gel caps at each end. Scale bars = 10 μm.

trifusiform with two constrictions along the length (rarely bifusiform with a single constriction), a single septum at the upper constriction, small, globose gelatinous caps at each end, hyaline. Conidiomata developing within leaf spots prior to the mature ascomata, immersed in host tissue, host tissue darker around the conidiomata, conidiomata globose, opening by a small, round pore through stomata, conidiomatal wall about 10 µm thick, comprising 5–6 layers of tangled hyphae 1.5–2.5 µm diam. with walls hyaline, thin. Wall near the opening of the conidioma up to 20 µm thick, comprising hyphae up to 6 µm diam., innermost cells lining the ostiole slightly elongated and periphysoid-like. Conidiomatal wall lined with conidiogenous layer. Conidiogenous cells 10–17 × 1.5–2 µm, cylindric, tapering slightly towards the barely differentiated apical conidiogenous locus; several conidiogenous cells held on a conidiophore, cylindric, 8–12 × 2–2.5 µm, hyaline. Conidia 16–24 × 0.8–1 µm filiform, straight to irregularly curved, 0–septate, hyaline.

Additional specimens examined—**NEW ZEALAND**: **Auckland**: Hauraki Gulf, Tiritiri Matangi Is., Ridge Track, on *Phormium tenax* living leaf, 28 Oct 2000, coll. E.H.C. McKenzie, R.E. Beever REB1978 (PDD 83472); Tiritiri Matangi Island, on *Phormium tenax* living leaf, 27 Oct 2000, coll. P.R. Johnston R1017 (PDD 72007); Piha, on *Phormium tenax* living leaf, 5 Oct 1972, coll. J.M. Dingley (PDD 60494); Piha, on *Phormium tenax* living leaf, 2 Apr 1956, coll. J.M. Dingley (PDD 60497); Piha, on *Phormium tenax* living leaf, 5 Sep 1960, coll. J.M. Dingley (PDD 60500); Piha, on *Phormium tenax* living leaf, Sep 1960, coll. R.F.R. McNabb (PDD 43290); Piha, on *Phormium tenax* living leaf, 5 Oct 1972, coll. J.M. Dingley (PDD 43312); Waitakere Swamp, on *Phormium tenax* living leaf, 3 Apr 1964, coll. J.M. Dingley (PDD 23268); Karekare, on *Phormium tenax* living leaf, 27 Apr 1971, coll. J.M. Dingley (PDD 60495); Anawhata, on *Phormium tenax* living leaf, 13 May 1972, coll. J.M. Dingley (PDD 60498). **Chatham Islands**: Rekohu, Rangaika Reserve, on *Phormium tenax* living leaf, 21 Nov 1992, coll. E.H.C. McKenzie, P.R. Johnston C80 (PDD 62689). **Coromandel**: Little Barrier Island, near East Cape, on *Phormium tenax* living leaf, 16 June 1984, coll. R.E. Beever, P.R. Johnston, E.P. Laracy (PDD 55303). **Nelson**: Tākaka Saddle, on *Phormium tenax* living leaf, 17 Nov 1970, coll. J.M. Dingley (PDD 60647). **Northland**: Maunganui Bluff Scenic Reserve, on *Phormium tenax* living leaf, 19 Oct 1987, coll. E.H.C. McKenzie, P.R. Johnston (PDD 48400); Whangaruru North Head, on *Phormium tenax* living leaf, 28 Jan 1988, coll. P.R. Johnston (PDD 54127); Waipoua Forest, Lookout Track, on *Phormium tenax* living leaf, 11 May 2017, coll. P.R. Johnston D2429 (PDD 108765); Three Kings Islands, Great Island, vic. light beacon, on *Phormium tenax* living leaf, 27 Nov 1997, coll. R.E. Beever REB 1565-2 (PDD 68427).

Notes: First collected in the 1950s, this fungus is common on living leaves of *Phormium tenax* in north New Zealand. Although its host occurs throughout New Zealand, no specimens have been yet been collected south of Nelson or the Chatham Islands.

Marthamyces maccormackii P.R. Johnst., **sp. nov.** Fig. 7

IF 556324

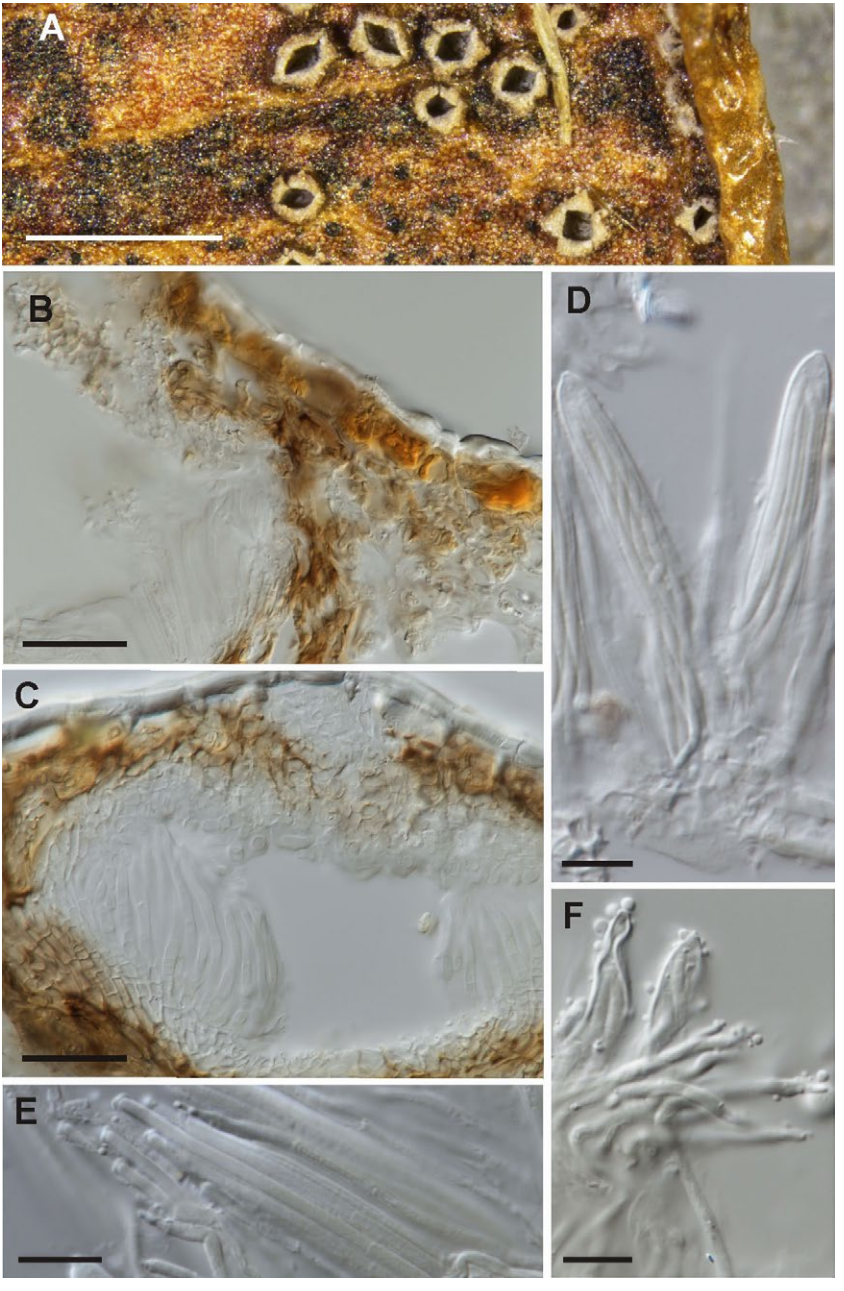
Differs from *M. emarginatus* by its darker ascomatal wall and from *M. metrosideri* by its rostrate ascus apex.

Type: Cook Islands: Rarotonga: Te Rua Manga, near summit, on *Metrosideros collina* fallen leaves, 28 Jun 2005, coll. P.R. Johnston RR392 (**holotype** PDD 112256; **ex-type culture** ICMP 15829).

Etymology: Named in honour of Gerald McCormack, director of the Cook Islands Biodiversity and Natural Heritage Trust, who provided the support needed to collect the Cook Islands specimens cited here.

Ascomata developing on recently fallen leaves, often associated with slightly paler areas on the leaf, initially appearing as a slightly raised dark spot, opening initially as a pore, then by three to four radiate slits, the covering host and fungal tissue folding back as small triangular flaps, the undersides of which are covered with a layer of white crystals, exposed hymenial surface with a layer of whitish crystals. Mature ascomata 0.3–0.5 mm diam., more or less circular in shape, covering tissue normally darkened, pale in some collections, hymenial surface remaining well below the surface of the host tissue. Ascomata subepidermal, immature ascomata in vertical section with a 50 µm thick covering layer comprising partially decomposed host epidermal cells and several layers of fungal tissue. The outermost, clypeus-like layer comprises 3–4 rows of tangled hyphae 2.5–3.5 µm diam., with hyphal walls dark brown, irregularly thickened, but this is lacking near the centre of the ascoma. The upper wall of the ascoma comprises several layers of globose to angular cells 3–5 µm diam. with walls thin, slightly pigmented, and this layer of cells is lined with a layer of downward-projecting periphysoids 2–3 µm diam., with walls thin, hyaline. In mature ascomata the upper wall develops clumps of crystals forming amongst the globose to angular cells. Lower wall of the ascoma 15–20 µm thick, comprising several layers of tangled hyphae 2.5–3.5 µm diam. with hyphal walls dark brown, irregularly thickened. Paraphyses 2 µm diam., with several short, tapering branches near apex 1–1.5 µm diam., paraphyses about the same length as the asci. Asci 75–95 × 7.5–9 µm, cylindric, tapering suddenly to small, rostrate apex, wall undifferentiated, 8-spored. Ascospores 50–70 × 1.5–2 µm, gelatinous caps at each end small, flattened, 1-septate, hyaline.

Additional specimens examined: **COOK ISLANDS**: **Rarotonga**: Cross Island walk, near Te Rua Manga, on *Metrosideros collina*, 30 Jun 2005, coll. P.R. Johnston RR611 (PDD 112250, culture ICMP 16155); track to Ikurangi, near the top, on *M. collina* fallen leaves, 16 Jan 2005, coll. P.R. Johnston RR315 (PDD 112258, culture ICMP 15831); track to Ikurangi, near the top, on *M. collina* fallen leaves, 4 Jul 2005, coll. P.R. Johnston RR635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(PDD 112260); Te Rua Manga, near summit, on *M. collina* fallen leaves, 5 Jul 2005, coll. P.R. Johnston RR650 (PDD 112255).

Notes—There are two *Metrosideros*-inhabiting species of *Marthamyces* in the Cook Islands. *Marthamyces maccormackii* has small, circular ascomata with a dark upper wall, macroscopically remarkably similar to *M. metrosideri* from New Zealand but phylogenetically quite distinct and also different in having a rostrate rather than rounded ascus apex. A second, sympatric *Marthamyces* species from the same host in the Cook Islands has larger, more angular, less deeply immersed, paler-walled ascomata with a yellow hymenial surface and is described below as *M. renga*. Microscopically the two Cook Island species differ in ascus shape. The two species often form in lesions adjacent to each other on the same leaves.

Marthamyces metrosideri P.R. Johnst., **sp. nov.** Fig. 8

IF 556325

Differs from *Marthamyces emarginatus* by its *Metrosideros* host preference, its darker upper wall of ascomata, and its ascus tapering gradually to rounded apex.

Type: New Zealand: Wellington: Wainuiomata Waterworks Catchment Area, on *Metrosideros robusta* fallen leaves, 19 Nov 1992, coll. P.R. Johnston R965 (**holotype** PDD 67458; **ex-type culture** ICMP 22625).

Etymology: based on host genus name.

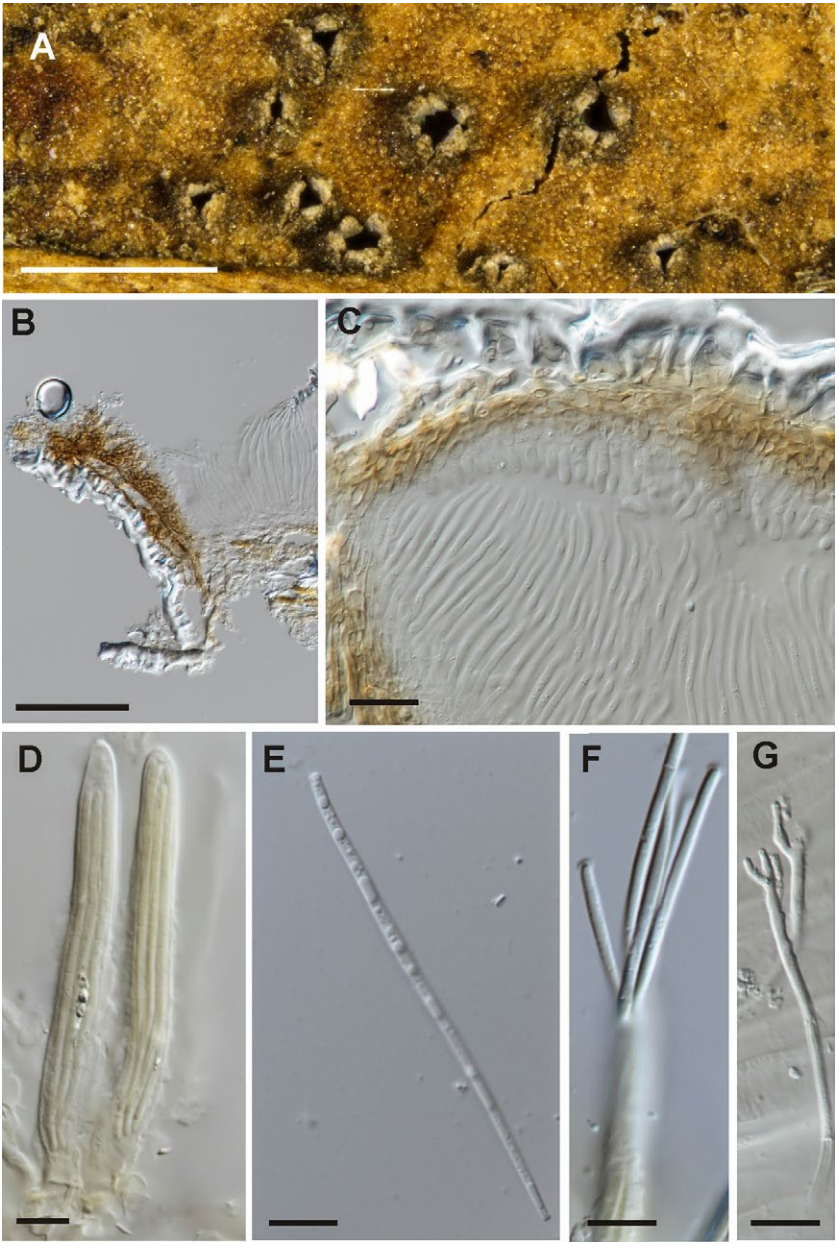
Ascomata developing within slightly paler areas on the lower surface of fallen leaves. Immature ascomata initially with appearance of small, darkened pustules. Mature ascomata round in outline, 0.3–0.4 mm diam., opening by several radiates slits, covering layer of host and fungal tissue folding back as 3–4 flaps lined with white crystals, exposing the white, pruinose hymenial surface. Ascomata subepidermal, in vertical upper wall of immature ascoma comprising 4–5 layers of angular to globose cells 3–5 µm diam., with walls thin, darkened, lined with layer of downward-projecting periphysoids, 15–30 × 3–3.5 µm, cylindric, unbranched, walls thin, hyaline. Lower wall of immature ascoma 20–35 µm thick, of several layers of hyphae 1.5–2.5 µm diam., with walls brown, slightly thickened, forming a loose textura intricata. Mature ascomata in vertical section with upper wall 70–100 µm thick, comprising a 10–30 µm wide layer of 3–5 µm diam. hyphae with cell walls thin, dark brown,

Figure 7. *Marthamyces maccormackii* (PDD 112256). A. Macroscopic appearance when dry; B. mature, opened ascoma in vertical section; C. Immature, unopened ascoma in vertical section; D. Asci; E. Flattened gel caps at top of ascospores; F. Paraphyses . Scale bars: A = 1 mm; B, C = 20 µm; D–F = 10 µm.

and a broad layer of crystals. Upper wall of mature ascomata lined with a layer of inward-projecting, hyaline, thin-walled periphysoids, individual elements shorter than in unopened ascomata, up to 10 µm long. Paraphyses 2–3 µm diam., with short side-branches 1–1.5 µm diam. near apex. Asci 70–105(–120) × 7–9.5 µm, subcylindric to subfusoid, tapering gradually to rounded to broadly rounded apex, wall undifferentiated at apex, 8-spored. Ascospores 45–85 × 2–3 µm, filiform, straight when released, tapering slightly and gradually towards the base, with small, flattened gelatinous caps at apex and base, 0–1-septate, hyaline.

Additional specimens examined: **NEW ZEALAND**: **Kermadec Islands**: Raoul Island, Denham Bay Track, on *Metrosideros kermadecensis*, 22 Sep 1988, coll. E.H.C. McKenzie (PDD 54664); Raoul Island, Blue Lake Track, on *M. kermadecensis*, 23 Sep 1988, coll. E.H.C. McKenzie (PDD 54666). **Northland**: Waipoua State Forest, Yakas Track, on *M. robusta*, 20 Oct 1987, coll. P.R. Johnston (PDD 48163); vic. Ōpononi, Waimamaku River mouth, on *M. excelsa*, 21 Oct 1987, coll. P.R. Johnston (PDD 53849); Whangaruru North Head, on *M. excelsa*, 28 Jan 1988, coll. P.R. Johnston (PDD 54117); Ahipara, Shipwreck Bay, on *M. excelsa*, 8 May 2017, coll. P.R. Johnston D2421 (PDD 111232). **Auckland**: Waitakere Ranges, Walker Bush, on *M. robusta*, 4 Aug 1982, coll. E.H.C. McKenzie, G.J. Samuels, P.R. Johnston R64 (PDD 43951); Huia Dam footbridge, on *M. excelsa*, 27 Apr 1982, coll. P.R. Johnston R52 (PDD 43952); Kaitarakihi Beach, on *M. excelsa*, 8 Mar 1983, coll. P.R. Johnston (PDD 43953); Piha Valley, Cowan Track, on *M. robusta*, 27 Apr 1983, coll. P.R. Johnston R209, G.J. Samuels, R.H. Petersen (PDD 43954); Mt Albert Research Centre, on *Metrosideros* sp., May 1983, coll. P.R. Johnston (PDD 43955); Kaitarakihi Beach, on *M. excelsa*, 20 Jul 1983, coll. P.R. Johnston (PDD 43958); Cornwallis Beach, on *M. excelsa*, 13 Apr 1984, coll. P.R. Johnston (PDD 49151). **Coromandel**: vic. Coromandel, 309 Road, Waiau Falls Scenic Reserve, on *M. robusta*, 25 Apr 1989, coll. P.R. Johnston (PDD 55341); Thames Coast, between Te Mata and Waikawau, on *M. excelsa*, 26 Aug 1999, coll. P.R. Johnston R1003, B.M. Spooner (PDD 70890); Tapu-Coroglen Road, 2 km Tapu side of summit, on *M. robusta*, 29 Aug 1984, coll. P.R. Johnston R552 (PDD 46194); North of Colville, vic. Ohinewai Stream, on *M. excelsa*, 27 Jan 1985, coll. P.R. Johnston (PDD 46775); Waihi, track N of beach, on *M. excelsa*, 9 May 2003, coll. P.R. Johnston (PDD 78201); Port Charles, between wharf and Big Sandy Bay, on *M. excelsa*, 26 Mar 1989, coll. P.R. Johnston (PDD 55293); Awaroa Stream, on *M. fulgens*, 12 Jun 1984, coll. P.R. Johnston (PDD 55294); Little Barrier Island, Titoki Point, on *M. excelsa*, 11 Jun 1984, coll. P.R. Johnston (PDD 45364); Little Barrier Island, near hut, on *M. excelsa*, 8 Apr 1988, coll. P.R. Johnston R795 (PDD 48768); Little Barrier Island, south of Te Wairere, on *M. excelsa*, 9 Mar 1974, coll. W.B. Kendrick (PDD 40728). **Gisborne**: Urewera National Park, Ngāmoko

Figure 8. *Marthamyces metrosideri* (A–C, E–G. PDD 111232; D. PDD 55341). A. Macroscopic appearance when dry; B. Mature, opened ascoma in vertical section; C. Immature, unopened ascoma in vertical section; D. Asci; E. Released ascospore; F. Apex of ascospores showing gel caps; G. Paraphyses. Scale bars: A = 1 mm; B, C = 20 µm; D–G = 10 µm.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Track, on *M. robusta*, 10 May 2001, coll. P.R. Johnston (PDD 74308); vic. Ruatāhuna, Mangapae, on *M. robusta*, 24 May 2005, coll. P.R. Johnston R1033, T. Hosoya (PDD 82920). **Taranaki**: Mt Egmont, Waiweranui Track, on *M. robusta*, 25 Apr 1983, coll. P.R. Johnston R274, G.J. Samuels, R.H. Petersen (PDD 43957). **Wanganui**: Kai Iwi, Bushy Park Reserve, on *M. robusta*, 15 May 1987, coll. P.R. Johnston (PDD 45587). **Nelson**: Karamea Bluff, Large Matai Track, on *M. robusta*, 25 May 1989, coll. P.R. Johnston, E.M. Gibellini (PDD 57159); Karamea, 1 km S Granite Creek Road, on *M. robusta*, 14 Apr 1983, coll. P.R. Johnston R262, G.J. Samuels, R.E. Beever (PDD 43956, culture ICMP 22624). **Buller**: vic. Greymouth, Point Elizabeth Walkway, on *M. robusta*, 1 May 1985, coll. P.R. Johnston R645, G.J. Samuels, L.M. Kohn (PDD 46961). **Westland**: Haast, Hāpuku River mouth, on *M. umbellata*, 11 May 2002, coll. S.R. Whitton, T. Atkinson (PDD 75509).

Notes—This common, *Metrosideros*-inhabiting fungus was previously identified as *M. emarginatus* (Johnston 1986, as *Propolis emarginata;* McKenzie & al. 1999, as *Propolis emarginata*). Based on published descriptions (e.g. Sherwood 1977), examination of the type specimen of *M. emarginatus*, and the features of the specimens from *Eucalyptus* from Australia deposited as PDD 81844, PDD 81845, and PDD 81846, the two species are very similar but slight, apparently consistent morphological differences (see diagnosis) are matched by the five transitions across the ITS1 and ITS2 regions.

Marthamyces renga P.R. Johnst., **sp. nov.** Fig. 9

IF 556326

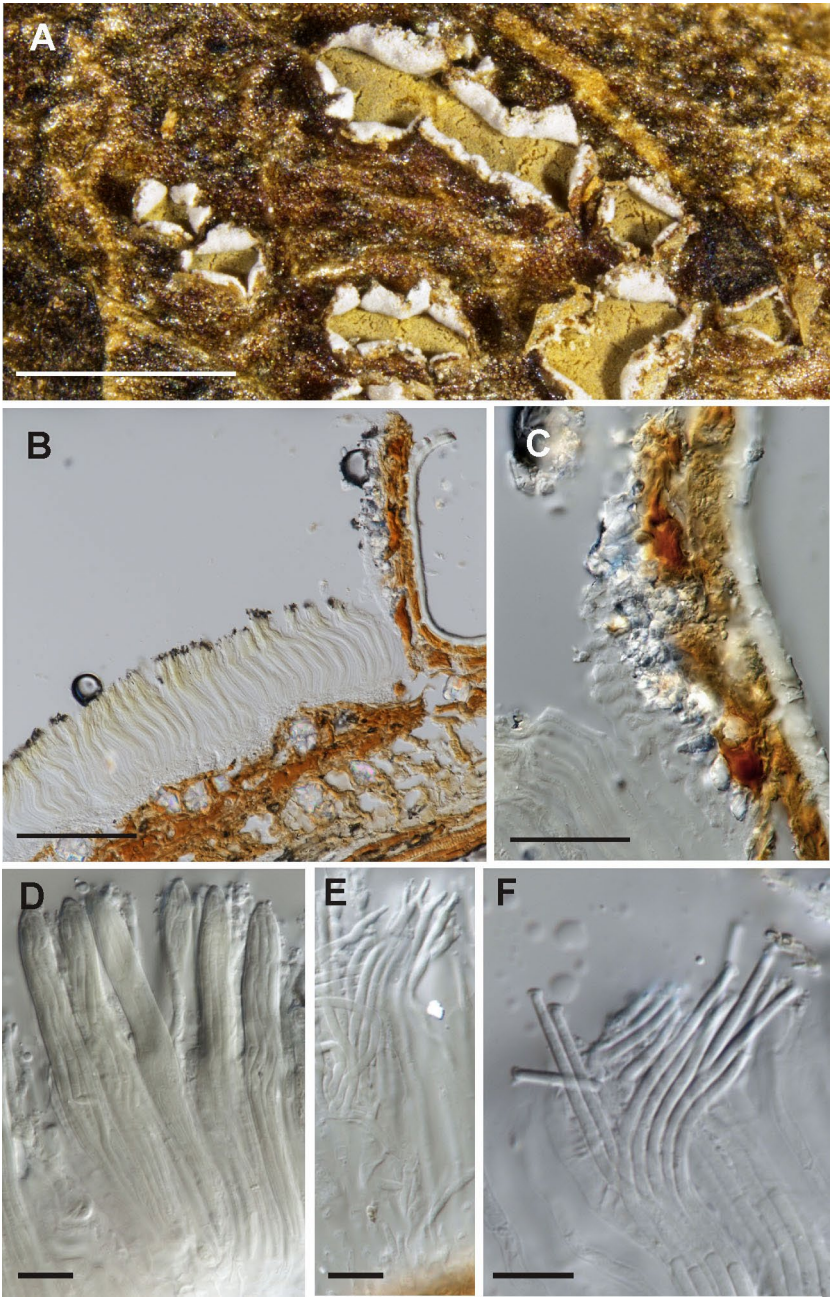
Differs from *Marthamyces emarginatus* by its larger, more angular, less deeply immersed ascomata, and its sharp contrast between the white crystals lining the upper wall and the yellow crystals on the hymenial surface.

Type: Cook Islands: Rarotonga: Raemaru Track, summit, on *Metrosideros collina* fallen leaves, 28 Jun 2005, coll. P.R. Johnston RR562 (**holotype** PDD 112263).

Etymology: renga, Cook Island Māori word for yellow, referring to the colour of the hymenial surface.

Ascomata developing within slightly paler areas on both the upper and lower surface of recently fallen leaves, initially appear as slightly raised patches, these splitting open by 3–4(–5) radiate slits, the covering host and fungal tissue folding back as small flaps, the undersides of which are covered with a layer of white crystals, the exposed hymenial surface crystalline, yellow. Mature ascomata 0.4–1.5 × 0.4–0.8 mm, angular, 3–5-sided. Ascomata subepidermal, in vertical section mature ascomata with a covering layer 50–60 µm thick,

Figure 9. *Marthamyces renga* (A–C. PDD 112263; D–F. PDD 112259). A. Macroscopic appearance when dry; B. Mature, opened ascoma in vertical section; C. Detail of upper wall of opened ascoma in vertical section; D. Asci; E. Paraphyses; F. Apex of ascospores with flattened gel cap. Scale bars: A = 1 mm; B = 100 µm; C–F = 10 µm.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comprising mostly partially broken-down cells of the host leaf tissue, together with crystals forming within a thin layer of more-or-less globose fungal cells with walls thin, hyaline, lined with a layer of broad-cylindric periphysoids, 10–20 × 4–6 µm, thin-walled, hyaline, unbranched. Lower wall 10–15 µm thick, comprising a compact layer of 3–4 µm diam. hyphae with cell walls hyaline, slightly thickened. Paraphyses 2–2.5 µm diam., with several short, tapering branches near apex 1–1.5 µm diam., intermixed with groups of small crystals, paraphyses about the same length as the asci. Asci 75–90 × 7–9.5 µm, cylindric, tapering slightly to rounded apex, wall undifferentiated, 8-spored. Ascospores rarely seen released, 1.5–2 µm wide, about 55–70 µm long, gelatinous caps at each end small, flattened, 1-septate, hyaline.

Additional specimens examined: **COOK ISLANDS**: **Rarotonga**: Te Rua Manga, on track near summit, on *Metrosideros collina* fallen leaves, 21 Jan 2005, coll. P.R. Johnston RR393 (PDD 112257; culture ICMP 15830); Te Kou, on track near summit, on *Metrosideros collina* fallen leaves, 19 Jan 2005, coll. P.R. Johnston RR380 (PDD 112259; culture ICMP 15827). Te Rua Manga, on track near summit, on *Vaccinium cereum* fallen leaves, 5 Jul 2005, coll. P.R. Johnston RR397 (PDD 112261). Te Rua Manga, on track near summit, *Vaccinium cereum* fallen leaves, 5 Jul 2005, coll. P.R. Johnston RR642 (PDD 112264). Te Rua Manga, on track near summit, on *Weinmannia samoensis* fallen leaves, 5 Jul 2005, coll. P.R. Johnston RR641 (PDD 112262).

Notes: A macroscopically distinctive species with a marked contrast in colours between the white crystals on the underside of the upper wall of the ascoma and the yellow crystals on the hymenial surface. Although common on *Metrosideros collina*, this species is not host-specialized and was found also on recently fallen leaves of *Vaccinium cereum* G. Forst. (*Ericaceae*) and *Weinmannia samoensis* A. Gray (*Cunoniaceae*), both south Polynesian endemic plant species found in Rarotonga in the same high-altitude plant communities as *Metrosideros*. See also notes under *M. maccormackii*.

Ramomarthamyces P.R. Johnst., **gen. nov.**

IF 556327

Differs from *Marthamyces* by its distinctly branched paraphyses.

Type species: *Propolis dracophylli* P.R. Johnst. [= *Ramomarthamyces dracophylli* (P.R. Johnst.) P.R. Johnst.]

Etymology: *ramo* = branch; refers to the branched paraphyses in these *Marthamyces*-like fungi.

Ascomata immersed in the host tissue, opening by several radiate slits to reveal the pruinose, crystalline hymenial surface. Ascus wall undifferentiated at the apex, ascospores filiform, paraphyses branched several times near the apex.

Notes: A genus in the *Marthamycetaceae*, but molecular phylogenetic analysis shows it to be phylogenetically distinct from other genera within the family (Fig. 1). The genetic difference is supported by a characteristic morphology, all species known for the genus having distinctly branched, rather than propoloid, paraphyses. *Marthamyces* is macro-morphologically similar.

Ramomarthamyces tuku P.R. Johnst., **sp. nov.** Fig. 10

IF 556333

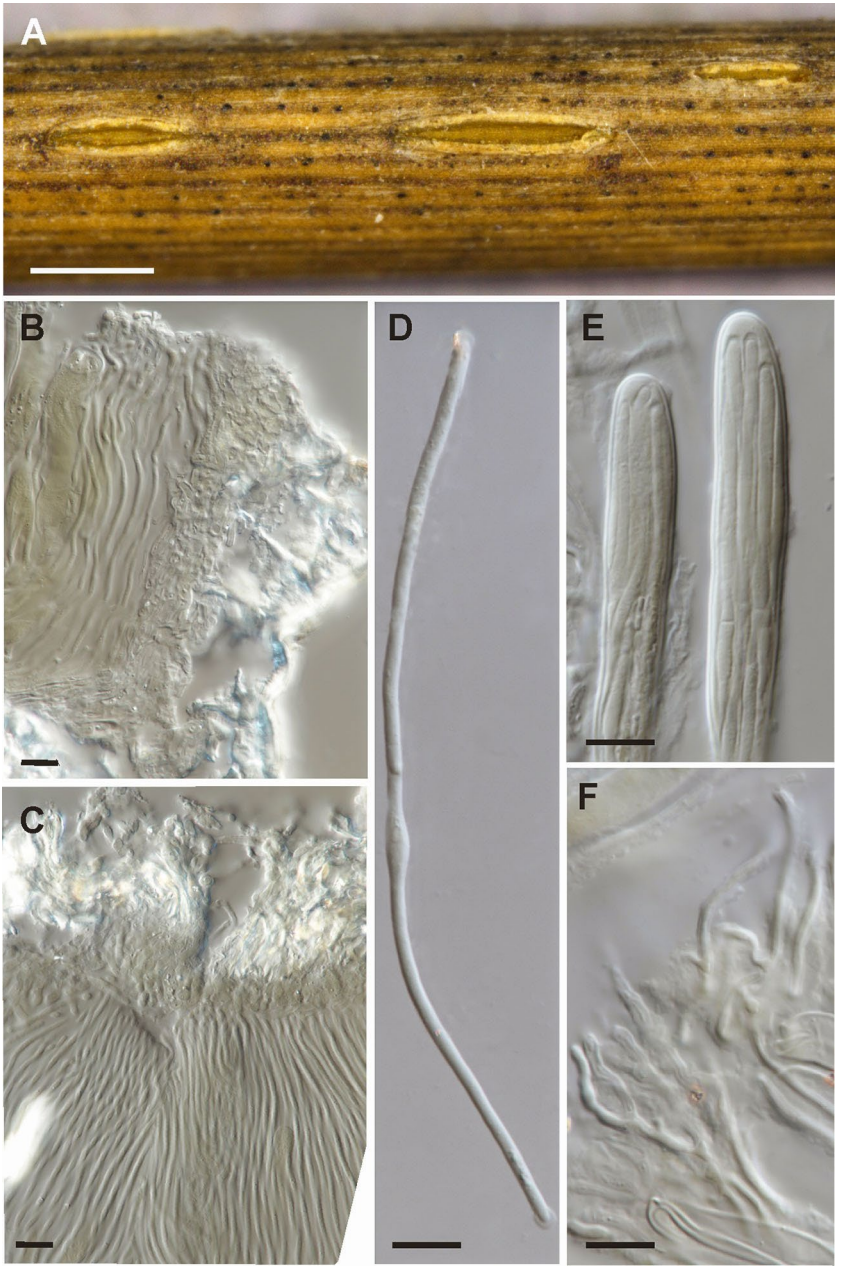
Differs from *Ramomarthamyces gilvus* by its *Juncaceae* host, its elongate ascoma, its ascospores with a swelling above the septum, its undifferentiated ascus wall, and its lack a well-developed layer of crystals amongst the paraphyses.

Type: New Zealand, Chatham Islands, Rekohu, Tuku Reserve, on *Juncus* sp., dead leaves, 19 Nov 1992, coll. P.R. Johnston C42, R911 & E.H.C. Mckenzie (**holotype** PDD 62161; **ex-type culture** ICMP 22562).

Etymology: tuku, based on type locality.

Ascomata developing on dead leaves, not associated with discoloured areas. Ascomata 0.5–1 × 0.2–0.3 mm, immersed in the leaf, opening by an elongate slit, covering layer slightly paler than the surrounding leaf tissue, sometimes with poorly developed crystalline layer near edge of opening slit, exposed hymenium translucent yellow, lacking obvious crystals. Ascomata intrahypodermal, in vertical section immature ascomata with a covering layer 50–70 µm thick, comprising most partly decomposed host cells intermixed with a poorly developed, clypeus-like layer of hyphae 3–5 µm diam. with walls thin, hyaline. Beneath the host cells is a 10 µm thick layer of narrow tangled hyphae with walls thin, hyaline, this layer lined with broad-cylindric periphysoids 10–15 × 4–5 µm, with walls thin, hyaline. Mature ascomata similar in vertical section but periphysoids more or less lost, and clumps of crystals forming amongst the hyphae of the upper wall near the opening slit. Lower wall 10–15 µm thick, comprising several rows of narrow, tangled hyphae with walls thin, hyaline. Paraphyses 1.5–2 µm diam., several times branched near the apex, extending 20–25 µm beyond asci. Asci 115–125 × 9–10 µm, cylindric, apex broadly rounded, wall undifferentiated at apex, 8-spored. Ascospores 110 × 2–3 µm, 1-septate, a small swelling 3.5–4 µm diam. immediately above the septum, otherwise not tapering, more or less globose gelatinous caps at each end, 3–3.5 µm diam.

Notes: Although known only from the type specimen, this is a clearly distinct species, both morphologically and phylogenetically. An inconspicuous fungus, it is likely to be widespread on *Juncus* in New Zealand. The closely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related *R. gilvus* is known from several cyperaceous hosts in Australia and it is possible that with more collections, *R. tuku* will be found to have a broader range of hosts. The New Zealand species *Marthamyces dendrobii* has similar distinctively shaped ascospores, with a small swelling immediately above the central septum, but differs in host, its ascoma having a dark upper wall, and its smaller ascospores.

Ramomarthamyces barbatus (P.R. Johnst.) P.R. Johnst., **comb. nov.**

IF 556329

≡ *Marthamyces barbatus* P.R. Johnst., Aust, Syst, Bot, 19: 137, 2006.

Note: Recombination based on both DNA sequence and morphological data.

Ramomarthamyces dracophylli (P.R. Johnst.) P.R. Johnst., **comb. nov.**

IF 556330

≡ *Propolis dracophylli* P.R. Johnst., New Zealand J. Bot. 24: 115, 1986.

≡*Marthamyces dracophylli* (P.R. Johnst.) Minter, Mycotaxon 87: 51, 2003.

Note: Recombination based on both DNA sequence and morphological data.

Ramomarthamyces gilvus (Rodway) P.R. Johnst., **comb. nov.**

IF 556331

≡ *Naemacyclus gilvus* Rodway, Pap. & Proc. Roy. Soc. Tasmania 1917: 107, 1918.

≡ *Marthamyces gilvus* (Rodway) P.R. Johnst., Aust. Syst. Bot. 19: 140, 2006.

Note: Recombination based on both DNA sequence and morphological data.

Discussion

Marthamyces harakeke is widespread and common as a leaf spot on *Phormium* in New Zealand. The earliest fungarium specimen of the fungus was collected in 1956 and deposited in PDD as *Propolis* sp., but with a note that the identification was uncertain. Later specimens were also referred to *Propolis* by several different mycologists. Although macroscopically the fungus is *Propolis*-like in having apothecia shallowly immersed in host tissue, a crystalline hymenial surface, and asci undifferentiated at the apex, there was always doubt about its identity because of the pathogenic lifestyle. It was not until DNA sequences were obtained from a specimen collected in 2017

Figure 10. *Ramomarthamyces tuku* (PDD 62161). A. Macroscopic appearance when dry; B. Mature, opened ascoma in vertical section; C. Immature, unopened ascoma in vertical section, showing periphysoids; D. Ascospore with a globose gel cap at each end; E. Apex of asci; F. Apex of paraphyses. Scale bars: A = 1 mm; B, C = 20 µm; D–F = 10 µm.

that its generic position was resolved. Today the genus used for this fungus and its relatives is *Marthamyces,* a generic name now used for several species that had been placed in *Propolis* in the past.

Both *Propolis* and *Marthamyces* were placed in *Rhytismataceae* at the time that Lantz & al. (2011) published a molecular phylogeny treating the *Rhytismatales* in depth. Their results showed the *Rhytismataceae* to be polyphyletic, and they regarded *Propolis* and *Marthamyces* as incertae sedis within the *Leotiomycetes*. With support from rDNA-based phylogenies, Baral (2015) placed *Propolis* and *Marthamyces* along with several other genera in a separate family, *Marthamycetaceae*, and more recently Johnston & al. (2019) erected the order *Marthamycetales*, based on a 15-loci analysis. In the present paper, species placed in the genus *Marthamyces* have been more intensively sampled with molecular data, and the genus was shown to be polyphyletic. As a result we created the genus *Ramomarthamyces* for species segregated from *Marthamyces* sensu stricto.

The phylogeny presented here shows a pathogenic lifestyle to have evolved more than once in the *Marthamycetaceae*. Along with *M. harakeke*, *M. culmigenus* (in a clade of species separate from that containing *M. harakeke*) and the *Cyclaneusma* species cause foliar diseases.

Marthamyces emarginatus was originally described from *Eucalyptus* from Victoria, Australia. *Marthamyces emarginatus*-like fungi are common on recently fallen *Eucalyptus* leaves in Australia, but the data presented here show that several closely related but phylogenetically distinct species occur on this substrate. Insufficient samples are available to determine whether there is a relationship between this diversity with respect to geography, or to phylogeny within *Eucalyptus*. Until the distribution of these fungi in Australian forests is better understood, a neotype cannot be selected for *M. emarginatus*.

Two GenBank accessions identified as *Coccomyces proteae* have ITS sequences that closely match *Marthamyces emarginatus*-like species (CBS 111703 as JN712451; CBS 111704 as JN712450; Fig. 2). Based on (Marincowitz & al. 2008) the morphology of *C. proteae* is typical of *Coccomyces*. It is possible that the putative *C. proteae* cultures from which these sequences were derived represent another, possibly undescribed, species of *Marthamyces* that grows on *Protea* leaves in South Africa. Note that another GenBank accession identified as *Coccomyces proteae* (JX089385 ex leaves of *Disterigma humboldtii* (*Ericaceae*) ex Puerto Rico) represents yet another *Marthamyces* species, this one belonging in the clade containing *M. maccormackii, M. renga,* and *M. culmigenus* (Fig. 2).

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